

Pliocene climate and seasonality in North Atlantic shelf seas

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This paper reviews North Atlantic shelf seas palaeoclimate during the interval 4–3 Ma, prior to and incorporating the ‘Mid-Pliocene warm period’ (*ca* 3.29–2.97 Ma). Fossil assemblages and stable isotope data demonstrate northwards extension of subtropical faunas along the coast of the Carolinas–Virginia (Yorktown and Duplin Formations) relative to the present day, suggesting a more vigorous Florida Current, with reduced seasonality and warm water extending north of Cape Hatteras (reconstructed annual range for Virginia 12–30°C). This interpretation supports conceptual models of increased meridional heat transport for the Pliocene. Sea temperatures for Florida (Lower Pinecrest Beds) were similar to or slightly cooler than (summers 25–27°C) today, and were probably influenced by seasonal upwelling of cold deep water. Reduced seasonality is also apparent in the Coralline Crag Formation of the southern North Sea, with ostracods suggesting winter sea temperatures of 10°C (modern 4°C). However, estimates from Pliocene bivalves (3.6–16.6°C) are similar to or cooler than the present day. This ‘mixed’ signal is problematic given warmer seas in the Carolinas–Virginia, and climate model and oceanographic data that show warmer seas in the ‘Mid-Pliocene’ eastern North Atlantic. This may be because the Coralline Crag Formation was deposited prior to peak Mid-Pliocene warmth.

Keywords: Pliocene; shelf seas; bryozoans; bivalves; seasonality

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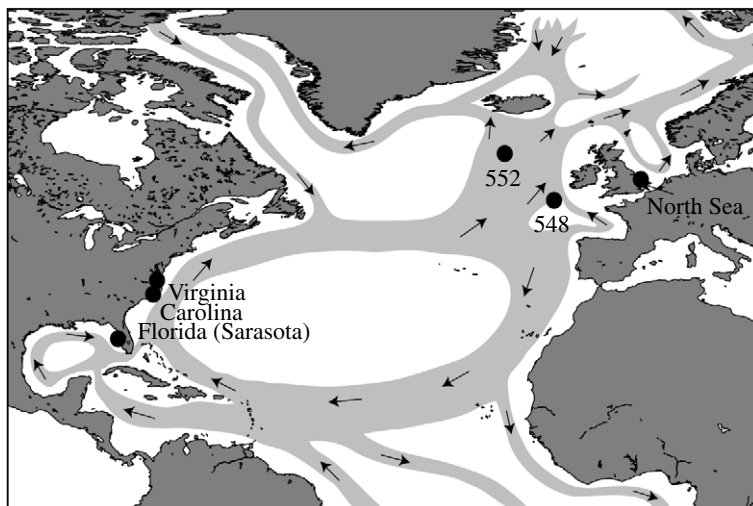


Figure 1. Geographical location of the Coralline Crag Formation, eastern England ('North Sea'), the Yorktown Formation of Virginia and lateral equivalents in the Carolinas, and the Tamiami Formation of Sarasota, Florida. DSDP sites 548 and 552 are also plotted (see text). Base map, courtesy of Harry Dowsett, shows modern surface ocean circulation (arrows).

1. Introduction

Continental shelf successions of Pliocene age in the North Atlantic are less complete than those of deep marine settings, and they are often bounded by unconformities that resulted from changes in sea level. Consequently, and in contrast to many deep marine sites, they do not provide a temporally complete record of Pliocene ocean conditions. Additionally, shelf successions tend to be preserved during global highstands in sea level (e.g. Dowsett & Cronin 1990), so that they record warm climate conditions but leave less evidence of cooler conditions. Sea-level lowstands, which may have been induced by cooler climates and increased polar ice sheet volumes, are often reflected in unconformities. Local controls on relative sea level may also generate unconformities in shelf successions. Despite these shortcomings, shelf successions can provide an important record of Pliocene sea temperatures, water masses and seasonality through the analysis of a range of fossil organisms, including bryozoans (e.g. O'Dea & Okamura 2000), bivalves (e.g. Ward *et al.* 1991; Hickson *et al.* 1999, 2000; Johnson *et al.* 2000), gastropods (Jones & Allmon 1995), ostracods (e.g. Hazel 1971; Wilkinson 1980; Wood *et al.* 1993; Cronin & Dowsett 1996), foraminifera (e.g. Jenkins *et al.* 1988; Dowsett & Wiggs 1992) and dinoflagellates (e.g. Head 1998; Louwye *et al.* 2004). In this paper we review evidence for Pliocene palaeoclimates in North Atlantic shelf sea successions deposited between approximately 4 and 3 Myr ago. These records are preserved in three celebrated Pliocene fossil-bearing successions (figures 1 and 2): the Coralline Crag Formation of Suffolk, eastern England (e.g. Balson *et al.* 1993; Gibbard *et al.* 1998); and the coastal plain sediments of the Carolinas–Virginia (e.g. Ward *et al.* 1991) and Florida (e.g. Cronin & Dowsett 1996).

The interval of the Pliocene between 4 and 2.5 Myr ago witnessed gradual global cooling and the enhancement of glaciation in the Northern Hemisphere (Zachos *et al.* 2001). Superimposed on this general cooling trend were intervals of greater warmth, most notably the 'Mid-Pliocene warm period', defined as that part of the Mid-Pliocene (Piacenzian) between *ca* 3.29 and 2.97 Ma (see Dowsett *et al.* 1999, 2005; Dowsett & Robinson 2006). Using a large database of oxygen isotope records from benthic and planktonic foraminifera at globally distributed sites, Mudelsee & Raymo (2005) demonstrated a long-term increase in ice volume from 3.6 to 2.4 Ma (equivalent to a 0.39‰ increase in seawater $\delta^{18}\text{O}$). There is an increase in the magnitude of variation in $\delta^{18}\text{O}$, from 0.2 ppt at 3.2 Ma to 0.3 ppt at 2.56 Ma, which records the increasing amplitude of fluctuation in ice volume, water salinity and/or water temperature, in turn reflecting climate change. The causal factors for global cooling during the Late Cenozoic remain unresolved, but may include a combination of tectonic uplift in the Tibetan Plateau and weathering-induced atmospheric CO_2 removal, and the closing of ocean gateways, most notably the Central American Seaway (CAS) and the Indonesian Seaway. Explanations for the 'Mid-Pliocene warm period', which lasted for approximately 300 000 years, revolve around elevated atmospheric $p\text{CO}_2$ levels (e.g. Dowsett *et al.* 1992; Haywood *et al.* 2005), increased ocean heat transport from the tropics to higher latitudes (e.g. Dowsett *et al.* 1992, 1996, 1999), reduced orography (e.g. Haywood *et al.* 2001), reduced size of the polar terrestrial ice sheets and sea ice cover (Haywood & Valdes 2004), or combinations of these factors (Dowsett *et al.* 2005, p. 6; see also Haywood & Valdes 2004, p. 373).

The mechanism of enhanced meridional ocean heat transport during the Mid-Pliocene warm period would have produced a weaker gradient in North Atlantic sea surface temperatures (SSTs) between the tropics and high latitudes. Thus, high-latitude SSTs would be warmer, while tropical and low-latitude SSTs would remain the same or cooler. By contrast, elevated concentrations of $p\text{CO}_2$ would cause warming at all latitudes (see discussion in Haywood *et al.* 2005). Organisms whose skeletal chemistry and morphology record a temperature signal throughout the year, including shelf-dwelling bryozoans and bivalves, offer the chance of determining seasonal SST gradients for the North Atlantic and thus provide additional data by which to investigate the forcing mechanism of Pliocene warmth.

The aims of this paper are to: (i) provide a summary correlation scheme for the Pliocene sequences of Florida, Virginia and the Carolinas in the eastern USA, and Suffolk, eastern England, indicating the formations that record the Mid-Pliocene warm period; (ii) summarize the range of palaeoclimate data from these rock successions; (iii) recalibrate some of the biogenic oxygen isotope data for palaeotemperature and compare these data with the latest climate model reconstructions for intervals of the Early (Zanclean) and Mid- (Piacenzian) Pliocene; and (iv) suggest future strategies for maximizing the data that can be gleaned from these successions.

2. Stratigraphical setting

The stratigraphical settings of the Pliocene successions in eastern England, Virginia–Carolinas and Florida are summarized in figure 2. The

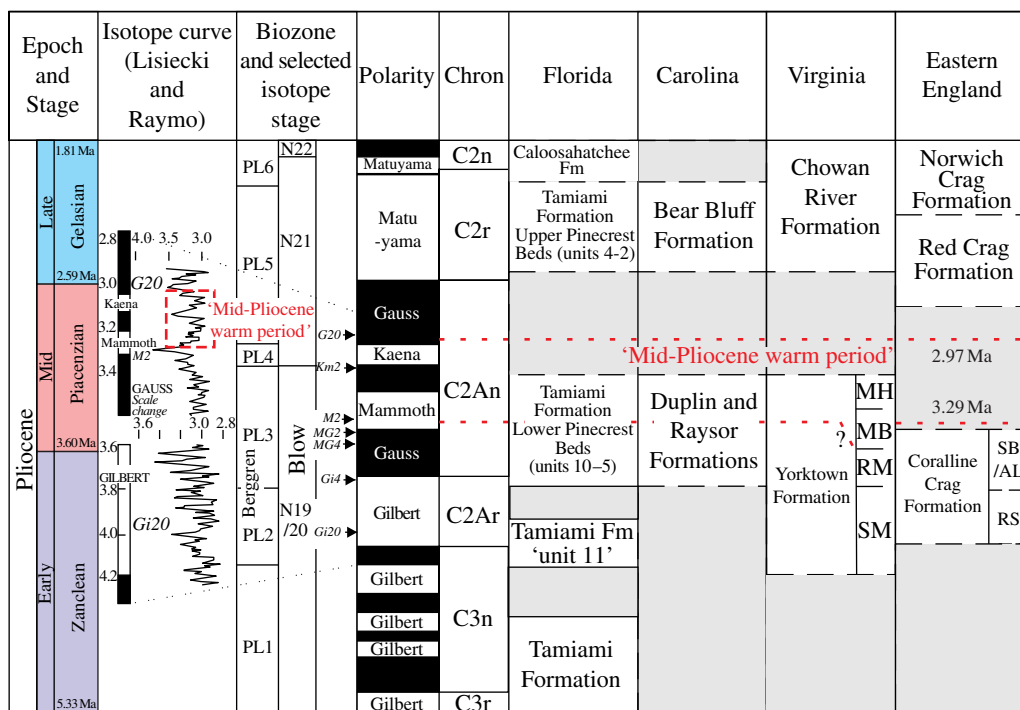


Figure 2. Pliocene stratigraphy of rock successions bordering the North Atlantic. Coralline Crag Formation comprises Ramsholt (RS), Aldeburgh (AL) and Sudbourne (SB) Members. Yorktown Formation of Virginia–Carolinas comprises Sunken Meadow (SM), Rushmere (RM), Morgart’s Beach (MB) and Moore House (MH) Members. The uppermost Moore House Member (MH) is restricted to southeastern Virginia ([Ward *et al.* 1991](#)). In the Tamiami Formation, Florida, unit 11 in the lower Tamiami Formation is considered of equivalent age to the Sunken Meadow Member (SM) of the Yorktown Formation ([Jones *et al.* 1991](#)). The overlying Lower Pinecrest Beds (units 10–5) are equivalent to the Morgart’s Beach/Rushmere/Moore House Members of the Yorktown Formation ([Cronin & Dowsett 1996](#)). For an exhaustive account of Tamiami Formation and ‘Pinecrest Beds’ nomenclature, including ‘unit 11’, see [Lyons \(1991\)](#). The ‘Mid-Pliocene warm period’ is also plotted, as is a selected segment of the isotope curve of [Lisiecki & Raymo \(2005\)](#). Plotted in the column for series and stages are absolute dates based on [Gradstein *et al.* \(2004\)](#) and some selected cool phases (glacials) of the Pliocene (Gi20, Gi4, MG4, MG2, M2, Km2, G20; see [Dowsett *et al.* 1999](#); [Lisiecki & Raymo 2005](#)).

palaeoenvironmental signal of the Yorktown, Tamiami and Coralline Crag Formations has been incorporated into interpretations of ‘Mid-Pliocene’ global palaeoclimate (e.g. Dowsett *et al.* 1994, table 1, 1996, 1999). However, these formations straddle time intervals that are longer than the *ca* 300 000 years of the Mid-Pliocene warm period (equivalent to the Kaena and Mammoth (*pars*) Subchrons, 3.29–2.97 Ma; see Dowsett *et al.* (1999) for definition), often including or entirely comprising successions deposited prior to that interval (figure 2). This longer interval records a much greater range of palaeoclimatic variation than is associated with the Mid-Pliocene warm period alone (e.g. Dowsett & Poore 1991; Cronin & Dowsett 1996; Mudelsee & Raymo 2005). It includes distinctly cooler phases (e.g. isotope stages Gi20 at 4 Ma and M2 at 3.3 Ma *sensu* Lisiecki & Raymo (2005)).

The Coralline Crag Formation of Suffolk rests unconformably on Eocene deposits of the London Clay Formation and is unconformably overlain by the Red Crag or Norwich Crag Formations. Typically 15–20 m thick, the Coralline Crag Formation yields age-diagnostic nanofossils (Jenkins & Houghton 1987), planktonic foraminifera (Jenkins *et al.* 1988) and dinoflagellates (Head 1998). Foraminifera, specifically *Neoglobobulimina atlantica* and *Globobulimina puncticulata*, suggest correlation with planktonic foraminiferal zones N19–N21 of Blow (1969; see Jenkins *et al.* 1988). Dinoflagellates suggest that the sequence straddles the Zanclean–Piacenzian boundary. Head (1998, fig. 2), based on a chain of correlation, depicted the youngest Coralline Crag Formation extending to the Mammoth Subchron (C2An2r) and the lower boundary of the formation within chron C2Ar. Presence of the dinoflagellate *Operculodinium tegillatum* in the Coralline Crag (Head 1997) indicates a maximum age greater than 3.5 Ma (Louwye *et al.* 2004, p. 363). Dinoflagellates suggest that the lower Ramsholt Member of the formation post-dates the Kattendijk Formation of Belgium, and many authors have correlated this unit with the Luchtbal Sands of that country (see Louwye *et al.* 2004, p. 373), suggesting an age of perhaps 4 Ma or greater (see De Schepper *et al.* 2004). The minimum age for the formation (at 3.4 Ma) suggests that it may completely pre-date the Mid-Pliocene warm period. Much of the biostratigraphical information available for the Coralline Crag Formation comes from the lower part (Ramsholt Member). The upper part (Sudbourne Member) largely comprises tidally generated cross-bedded calcarenites in which fossils are winnowed, variably transported and abraded. Importantly, the Ramsholt Member has not suffered the wholesale aragonite dissolution that has afflicted the Sudbourne Member and the laterally equivalent Aldeburgh Member (Balson 1983). This is very significant from the perspective of reconstructing accurate sea temperatures from stable oxygen isotope data preserved in biogenic carbonates in the Coralline Crag Formation.

The Yorktown Formation of the Carolinas–Virginia is unconformity bound, overlying rocks of the Miocene Eastover Formation and succeeded by the Late Pliocene Chowan River Formation (Ward & Powars 2004). It comprises four members, representing three transgressive pulses, the middle represented by the Rushmere/Morgart's Beach Members. The uppermost Moore House Member is restricted to southeastern Virginia (Ward *et al.* 1991). Yorktown Formation stratigraphy and its lateral equivalents are tied with the global planktonic foraminiferal scheme of Berggren (1973; see Dowsett & Wiggs 1992; also Dowsett & Cronin 1990), indicating that the succession equates to zones PL1b–PL3 (figure 2). Dowsett & Wiggs (1992) estimated that the Yorktown Formation might represent approximately 1 Myr of deposition, between approximately 4 and 3 Myr ago, though they favoured an age towards the younger part of that range. Magnetostratigraphy suggests that the upper boundary of the formation in Virginia equates to the Kaena or Mammoth Subchron (Cronin *et al.* 1994). Ward *et al.* (1991) considered the Duplin and Raysor Formations of the Carolinas to be lateral equivalents of the Rushmere/Morgart's Beach Members.

'Unit 11' in the lower Tamiami Formation of Florida is considered to be of approximate equivalent age to the Sunken Meadow Member of the Yorktown Formation (see Allmon *et al.* 1996, fig. 10.2; Cronin & Dowsett 1996). The overlying Lower Pinecrest Beds ('units 10–5', see Allmon *et al.* 1996) represent a major transgression equivalent to the Rushmere/Morgart's Beach/Moore House

Members of the Yorktown Formation (Cronin & Dowsett 1996) and to the Duplin and Raysor Formations of the Carolinas (see Jones *et al.* 1991, p. 643). Magnetochronology suggests that at least part of the Lower Pinecrest Beds may have been deposited during the Mammoth or Kaena Subchrons (Jones *et al.* 1991; Cronin & Dowsett 1996). The Upper Pinecrest Beds (units 4–2, see Allmon *et al.* 1996 and references therein) are separated by a hiatus, and palaeomagnetic data suggest correlation to the Matuyama Chron, and to the Chowan River Formation of southeastern Virginia and the northeastern Carolinas (Jones *et al.* 1991; Dowsett & Cronin 1996; figure 2).

3. Modern marine shelf setting adjacent to the selected fossil sites

The English and North American rock successions preserve a record of Pliocene climate in North Atlantic shelf sea settings across 25° of latitude in subtropical to temperate climes (modern latitudinal range *ca* 52° N to 27° N; see figure 1) over a time interval that may encompass a million years (figure 2). The formations record local acmes of marine conditions during Pliocene times that may therefore correlate with eustatic sea level and regional temperature maxima. It is thus reasonable to assume that the palaeoclimatic signature of fossil organisms will provide a fair comparison with climatic acmes from more open ocean settings at the same latitudes, and this has been supported by comparative studies (see Dowsett & Wiggs 1992; Cronin & Dowsett 1996). Modern North Atlantic Ocean surface-water circulation is dominated by the northward flow of the Gulf Stream, beginning life as the Florida Current flowing northwards from the Florida Straits to Cape Hatteras in North Carolina (35°13' N, 75°32' W). Beyond Cape Hatteras this warm water current flows away from the continental shelf, becoming the Gulf Stream (figure 1).

On the east coast of North America, the sharpest modern faunal boundary occurs at Cape Hatteras (e.g. Roy *et al.* 1998), defining the junction between subtropical and mild temperate zones. The gradient of temperature change northwards from Cape Hatteras is steep. At Cape Hatteras summer sea temperatures reach *ca* 26–27°C (source <http://www.nodc.noaa.gov/dsdt/cwtg/satl.html>, November 2007), with winter temperatures averaging approximately 10°C for December–February. A little to the north at Cape Charles in Virginia (37°10.0' N, 75°59.3' W), summer temperatures are similar to Cape Hatteras (25.5°C), but winter temperatures drop to 4.4°C (December–February average; data from <http://www.nodc.noaa.gov/dsdt/cwtg/satl.html>, November 2007). Importantly, Cape Hatteras lies midway between two of the main fossil localities reviewed here, in Virginia and the Carolinas (figure 1). Further to the south in the subtropics, winter and summer temperatures off southwest Florida, at depths comparable to those in which the Pinecrest Beds were deposited, are approximately 16 and 27°C, respectively (Cronin & Dowsett 1990, 1996), though surface temperatures are warmer than this (table 1).

The modern southern North Sea Basin is a shallow (generally less than 40 m) and unstratified body of water with little salinity variation (34–35 ppm), though in coastal regions salinity may be somewhat lower as a result of river input. Modern seasonal temperature variations in the southern North Sea range from winter temperatures of 4°C, to summer temperatures of 17°C (see Hickson *et al.* 1999; Swertz *et al.* 1999).

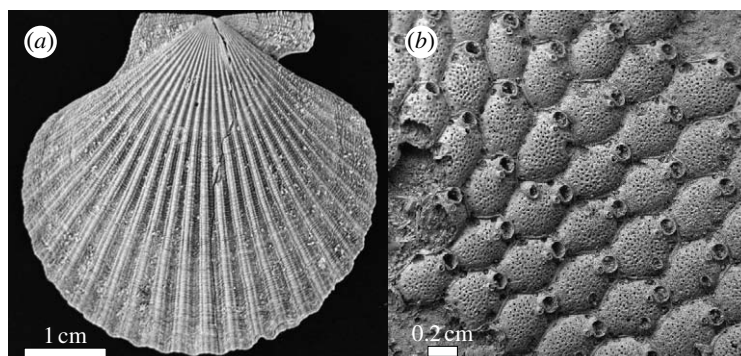


Figure 3. (a) The queen scallop *A. opercularis* used to establish sea temperatures in the Coralline Crag Formation of Suffolk, England, and (b) the bryozoan *Microporella* aff. *ciliata*, a potential source of MART data, from the Tamiami Formation, Sarasota, Florida.

4. Fossil recorders of Pliocene climate on the marine shelf

Existing palaeoenvironmental data from Pliocene molluscs, ostracods and bryozoans in the North Atlantic region are summarized in [table 1](#), together with the original absolute temperature values determined from analysis of oxygen isotopes in biogenic carbonates.

(a) Molluscs

Pliocene deposits of the coastal plain of eastern North America and England contain rich mollusc assemblages (e.g. [Harmer 1898](#); [Krantz 1990](#); [Ward *et al.* 1991](#); [Jones & Allmon 1995](#); [Hickson *et al.* 1999](#); [Johnson *et al.* 2000](#)). In the eastern North Atlantic, the extant queen scallop *Aequipecten opercularis* ([figure 3a](#)) is a fast-growing bivalve that also occurs in Pleistocene and Pliocene deposits. Today this species inhabits marine settings from low water to 183 m depth and has an overall temperature tolerance of 5°C (winter minimum) to 24°C (summer maximum) (see [Johnson *et al.* 2000](#)). It is tolerant only of small fluctuations in marine salinity, and is not found in sequences deposited under strong fluvial influence. Experimental work shows that the calcitic outer part of the shell forms in isotopic equilibrium with seawater, making it a valuable palaeothermometer for ancient sequences (e.g. [Hickson *et al.* 1999, 2000](#)).

On the east coast of the USA well-preserved examples of the gastropods *Turritella gladeensis* and *Turritella apicalis* and the bivalves *Mercenaria campechiensis* and *Carolinapecten eboreus* from the Lower Pinecrest Beds of Florida were analysed for stable isotopes by [Jones & Allmon \(1995\)](#). [Krantz \(1990\)](#) analysed the stable isotopic composition of the extinct pectinid bivalves *Chesapecten jeffersonius*, *C. madisonius* and *C. eboreus* from the Yorktown Formation. In both of these studies sea temperatures were estimated from $\delta^{18}\text{O}$ values (see [table 1](#)). [Elliot *et al.* \(2003\)](#) demonstrated that growth rates in modern *Mercenaria* from the east coast of North America are reduced or strongly interrupted in waters below 8–10°C, while there is a summer growth break in warm waters ([Quitmyer & Jones 1997](#)), so that these bivalves may not record the full amplitude of seasonal temperature variation.

Table 1. Oceanographic data for sites in eastern England (Suffolk), Virginia, the Carolinas and Florida. (Present SSTs for the east coast of the USA are from <http://www.nodc.noaa.gov/dsdt/cwtg/sat.html> (downloaded on November 2007; these sea temperatures are based on historical data collected from the given locations, Cape Charles, Cape Hatteras and Miami Beach). Sea temperature data for the southern North Sea are from Swertz *et al.* (1999). Oxygen isotope data are from molluscs, seawater $\delta^{18}\text{O}$ estimates and temperature calculations are based on data in Krantz (1990) for Virginia, Jones & Allmon (1995) for Florida, and Johnson *et al.* (2000) for eastern England. Note that for temperature calculations from the bivalves, there is a slight possibility that the lowest and highest temperatures might have been missed by less-than-100% sampling. However, while summer maxima might have been a little higher, winter minima might equally have been a little lower. This pertains to the data of table 2 also. The maximum estimated range of Pliocene sea temperature variation is based on records from foraminifera, ostracods and molluscs at the various sites. Estimates of Pliocene temperature from ostracods are singled out, and are based on Wilkinson (1980) and Wood *et al.* (1993) for Suffolk, Hazel (1971) for Virginia, Cronin & Dowsett (1990) for Carolina, and Cronin & Dowsett (1996) for Florida. The table shows the marked change in seasonal change in temperature compared with the present day for the east coast of the USA north of Cape Hatteras, with much warmer winter temperatures typifying the Pliocene.)

modern latitude/ locality	modern SST range (°C)	modern seasonal range (°C)	maximum seasonal range of Pliocene temperature (°C) (forams, ostracods and molluscs)	ostracod Pliocene temperature range (°C)	estimated Pliocene seasonal range (°C)	seawater $\delta^{18}\text{O}$ estimate used in temperature calculations	maximum seasonal range of Pliocene sea temperatures from molluscs (°C)	selected Pliocene sea temperatures from molluscs (°C)
Suffolk 52°16' N	4–17 (southern N Sea)	13	5.5–24 (Coralline Crag, all lithological members)	10–24	6.6 MART (range 4.6–8.9) bryozoans	calculations where no ice volume correc- tion was applied –0.2 to –0.5‰	6.5–16.2	6.5–16.2 <i>Aequipecten opercularis</i> (two specimens, with no ice correction)
Virginia 37°10' N	4.4–25.5 (Cape Charles)	21	8.2–23.9 (MH, Yorktown)	12.5–22.5	11 ($\delta^{18}\text{O}$ of to –1.4 + 1.3‰ in <i>C. eboreus</i>) with minimum ice volume correction	–0.2 to –0.5‰ applied	8.2–23.9	8.9–23.9 <i>Chesapeake madisonius</i> (two specimens) and 10.1–21.1 <i>Carolina- pecten eboreus</i>
Virginia 37°10' N	4.4–25.5 (Cape Charles)	21	6.8–25 (RM, MB, Yorktown)	12.5–25	14.3 ($\delta^{18}\text{O}$ of –1.9 to +1.6‰ in <i>C. madiso- nius</i>) with minimum ice volume correction	–0.3 to –0.6‰	6.8–22.9	8.6–22.9 <i>Chesapeake madisonius</i> and 7.9–13.5 <i>Carolina- pecten eboreus</i> (both with minimum ice volume correc- tion)

(Continued.)

Table 1. (*Continued.*)

modern latitude/ locality	modern SST range (°C)	modern seasonal range (°C)	maximum seasonal range of Pliocene temperature (°C) (forams, ostracods and molluscs)	ostracod Pliocene temperature range (°C)	estimated Pliocene seasonal range (°C)	seawater $\delta^{18}\text{O}$ estimate used in temperature calculations	maximum seasonal range of Pliocene sea temperatures from molluscs (°C)	selected Pliocene sea temperatures from molluscs (°C)
Virginia 37°10' N	4.4–25.5 (Cape Charles)	21	7.1–20 (SM, York- town)	10–20	9.5 ($\delta^{18}\text{O}$ of -0.8 to $+1.6\%$ in <i>C. jeffersonius</i> shell) with minimum ice volume correc- tion	-0.3 to -0.4%	7.1–19.8	7.5–19.8 <i>Chesapecten</i> <i>jeffersonius</i> (two specimens, with minimum ice volume correc- tion)
Carolina 35°13' N	10–26.6 (Cape Hatteras)	16	18–26 (Duplin)	18–26	sub-tropical	no data	no data	no data
Florida 25°47' N	23–30 (Miami Beach)	7	6.9–25.7 (Lower Pinecrest Beds unit 6/7)	18–26	7.8–9.2 (<i>M. cam- pechensis</i>) or 9.3 (<i>Turritella</i>) both with no ice volume correction	-0.3 to -0.6% , and some with no ice volume correction	6.9–25.7	14.2–24.3 <i>Merce- naria campe- chensis</i> (two specimens) and 16.4–25.7 <i>Turritella</i> <i>apicalis</i> (both ranges based on calculations with no ice volume correction)

(b) *Bryozoans*

Cheilostome bryozoans are widespread in Pliocene deposits. These colonial benthic invertebrates have encrusting, erect or free-living colonies that are typically sessile (figure 3b). Bryozoans have a global distribution in marine shelf environments. Cheilostome colonies are composed of asexually budded zooids with calcite, aragonite or biimineralic skeletons. Zooid size at the time of budding is determined by ambient water temperature, smaller zooids forming in warmer waters (O'Dea & Okamura 2000 and references therein). This inverse correlation between zooid size and temperature appears to occur irrespective of food levels, reproductive state, or the overall rate of growth within colonies (e.g. O'Dea & Okamura 1999). Colonies growing in highly seasonal environments will therefore show a greater variance in zooid size than those in environments experiencing low seasonality. O'Dea & Okamura (2000) used this relationship to interpret mean annual range of temperature (MART) experienced by colonies, calibrating the relationship in modern bryozoans (see table 1).

(c) *Microfauna and flora*

Numerous microfossils are present in Pliocene shelf sequences, including ostracods (e.g. Hazel 1971; Wood *et al.* 1993; Cronin & Dowsett 1996), foraminifera (e.g. Dowsett & Wiggs 1992) and dinoflagellates (Head 1998), which have been used for reconstructing water temperature and ocean currents.

5. Diagnostic predictions of seawater $\delta^{18}\text{O}$ from Early and Mid-Pliocene climate model simulations

In this paper we have recalculated sea temperatures from some of the existing published data for $\delta^{18}\text{O}$ from molluscs (see table 2). An important consideration in calculating ancient SSTs using the $\delta^{18}\text{O}$ signal is the $\delta^{18}\text{O}$ value of seawater ($\delta^{18}\text{O}_{\text{sw}}$). The local or regional $\delta^{18}\text{O}_{\text{sw}}$ is a function of the global mean composition as well as geographical variations caused by the combined effects of changes in evaporation–precipitation patterns, runoff (in coastal regions), and ocean circulation patterns (Zachos *et al.* 1994; Schmidt 1998). To assess the relative importance of changes on the $\delta^{18}\text{O}_{\text{sw}}$ signal for the Pliocene, we use diagnostic $\delta^{18}\text{O}_{\text{sw}}$ predictions derived from fully coupled ocean–atmosphere general circulation model (OAGCM) simulations, using the UK Meteorological Office Model (HadCM3 GCM), for intervals of the Early and Mid-Pliocene. Both of the simulations derive their boundary conditions from the USGS PRISM2 dataset (Dowsett *et al.* 1999). They incorporate a correction for the reduced polar ice volume of the Pliocene. The only difference between these simulations is that the CAS is specified as open (to a depth of 350 m) in the Early Pliocene experiment. Results from these simulations have been published previously in Lunt *et al.* (2008; Early Pliocene) and Haywood *et al.* (2007; Mid-Pliocene). The response of these models to a closing of the CAS is bipolar, with a warming in the Northern Hemisphere and cooling in the Southern Hemisphere. Maximum warming (*ca* 7°C) in the Northern Hemisphere occurs in the North Atlantic (figure 4). However, the change in the global annual mean

Table 2. Recalibrated Pliocene sea temperature estimates using published data for bivalves from the Pliocene of eastern England (Johnson *et al.* 2000), Virginia (Krantz 1990) and Florida (Jones & Allmon 1995). (Temperatures for calcitic bivalves are calculated using the equation of O’Neil *et al.* 1969; $T^{\circ}\text{C}=16.9-4.38(\delta^{18}\text{O}_c-\delta^{18}\text{O}_w)+0.10(\delta^{18}\text{O}_c-\delta^{18}\text{O}_w)^2$) and those of aragonite bivalves use the equation of Grossman & Ku (1986) in the form used by Schöne *et al.* (2005; $T^{\circ}\text{C}=20.6-4.34(\delta^{18}\text{O}_c-(\delta^{18}\text{O}_w-0.2\text{‰}))$). Diagnostic predictions of Pliocene seawater $\delta^{18}\text{O}$ values are derived from fully coupled OAGCM simulations for the Early and ‘Mid’-Pliocene (see text). Sea temperatures for Virginia are somewhat warmer than calculated by Krantz (1990), while those of eastern England and Florida are similar to previously published calculations. Carré *et al.* (2005) have suggested that the Grossman and Ku equation does not describe the oxygen fractionation of all bivalves. In the column for the modern seasonal range of sea temperatures, the values for Cape Charles in Virginia are from <http://www.nodc.noaa.gov/dsdt/cwtg/satl.html> (downloaded on November 2007), those for Florida are from Cronin & Dowsett (1990, 1996), and those for the North Sea are from Swertz *et al.* (1999). In the right-hand column, calculations for winter and summer difference in sea temperature between Pliocene and modern are based on the temperatures shown in italics in columns 8 and 9.)

fossil locality	mollusc species	mollusc $\delta^{18}\text{O}$	fossil identifier (from original papers)	latitude used in seawater calculation	Early Pliocene model predicted seawater $\delta^{18}\text{O}$	‘Mid-Pliocene’ model predicted seawater $\delta^{18}\text{O}$	revised mollusc temperatures for ‘Mid-Pliocene’ scenario (°C)	revised mollusc temperatures for Early Pliocene scenario (°C)	modern temperature range (°C)	winter (w) and summer (s) differences, Pliocene – modern (°C)
Virginia (SM)	<i>C. jeffersonius</i> (calcite)	1.5 to –1.2	KING-CJ	37.1° N 72.5° W	0.7	1.1	14.1–26.3	12.4–24.4	4.4–25.5	8 (w) and –1.1 (s)
Virginia (RM/MB)	<i>C. jeffersonius</i> (calcite)	1.6 to –1.9	BB-CM	37.1° N 72.5° W	0.7	1.1	13.6–29.7	12–27.7	4.4–25.5	7.2 (w) and 4.2 (s)
Virginia (MH)	<i>C. jeffersonius</i> (calcite)	1.3 to –2	YAD-CM2	37.1° N 72.5° W	0.7	1.1	14.9–30.1	13.2–28.2	4.4–25.5	10.5 (s) and 4.6 (w)
Florida (unit 6/7)	<i>M. campechiensis</i> (aragonite)	1.8 to –0.25	MC130	27.4° N 82.5° W	0.9	1.02	16.9–25.2	15.8–24.7	16–27	0.3 (w) and –1.8 (s)
Florida (unit 6/7)	<i>M. campechiensis</i> (aragonite)	1.7 to –0.75	MC121	27.4° N 82.5° W	0.9	1.02	16.8–27.4	16.3–26.9	16–27	0.8 (w) & 0.4 (s)
Suffolk (CC)	<i>A. opercularis</i> (calcite)	2.4 to 0.7	UD 52796	53.5° N 2° E	0.09	0.14	6.5–13.4	6.3–13.2	4–17	2.3 (w) and –3.8 (s)
Suffolk (CC)	<i>A. opercularis</i> (calcite)	1.7 to –0.10	UD 52797	53.5° N 2° E	0.09	0.14	9.1–16.6	9.1–16.6	4–17	5.1 (w) and –0.4 (s)

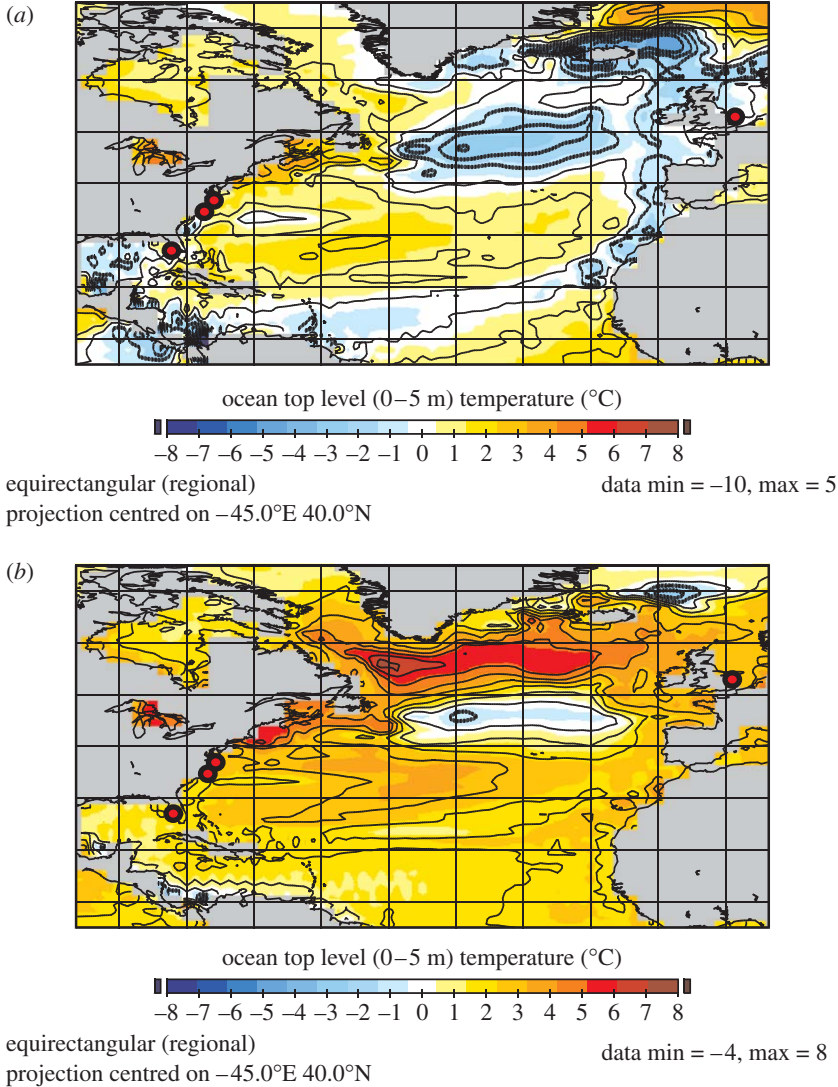


Figure 4. Climate model predictions showing change in annual mean ocean top level (0–5 m) temperatures (a) between the Early Pliocene and pre-industrial, and (b) between the ‘Mid-Pliocene warm period’ and pre-industrial, for the North Atlantic region. Red dots mark, from north to south, Florida, Carolinas, Virginia and southern North Sea (see also figure 1). Warmer conditions are demonstrated off the coast of the Carolinas–Virginia for the ‘Mid-Pliocene’, which are supported by fossil data from these areas (see tables 1 and 2).

temperature is small (*ca* 0.25°C), which is consistent with the primary response of the system to the closure of the CAS being a reorganization of ocean circulation. There is no large seasonal signal in the response. The bipolar signal persists with a similar magnitude throughout the year (Lunt *et al.* 2008). The termination, or restriction, of the flow of surface waters through the CAS intensifies North Atlantic thermohaline circulation. This change relates to the cessation (or reduction) of the flow of relatively fresh surface and sub-surface

waters from the Pacific into the Atlantic, which reduced the buoyancy of North Atlantic surface waters, leading to increased rates of North Atlantic Deep Water (NADW) formation. This increase in NADW formation is associated with a strengthened flow of the western boundary currents in the North Atlantic (the Gulf Stream), and an increase in northward heat transport.

Model calculated values for $\delta^{18}\text{O}_{\text{sw}}$ are an attempt to capture longitudinal and latitudinal changes as a function of climate, and are based on precipitation minus evaporation ($P-E$) estimates derived from the general circulation model (GCM). Present-day observed $\delta^{18}\text{O}_{\text{sw}}$ (Schmidt 1998; Schmidt *et al.* 1999; Bigg & Rohling 2000) is calibrated against observed $P-E$ (ECMWF reanalysis data, from the European Centre for Medium-Range Weather Forecasts) for the Atlantic Ocean. The resulting formula (see below) is used to predict $\delta^{18}\text{O}_{\text{sw}}$ gradients for the Pliocene. Atlantic calibration:

$$\delta^{18}\text{O}_{\text{sw}} = 0.24 - 0.008(P - E), \quad r^2 = 0.7.$$

$P-E$ is given in units of cm yr^{-1} .

In addition to $P-E$ we have also calibrated $\delta^{18}\text{O}_{\text{sw}}$ against salinity (Levitus & Boyer 1994). This increased the r^2 value to 0.9 but did not significantly change the diagnostic predictions of $\delta^{18}\text{O}_{\text{sw}}$ generated using $P-E$. Nevertheless, it is important to recognize that the use of a salinity: $\delta^{18}\text{O}$ or $P-E$: $\delta^{18}\text{O}$ co-variation from present-day observations as a diagnostic for the $\delta^{18}\text{O}$ composition of seawater during the Early or Mid-Pliocene is complicated by the fact that latitudinal temperature gradients are steeper today than they were during the Pliocene, a reflection of cooler temperatures in polar regions, which result in different patterns of Rayleigh distillation and hence different $\delta^{18}\text{O}$ values in the hydrological cycle (Rohling & Bigg 1998; Rohling 2000).

6. Warm and cool signals in the Pliocene of the southern North Sea

The Pliocene rocks of eastern England comprise shallow marine silts, sands and shell-rich sands deposited on the western margin of the southern North Sea Basin (figure 1). This basin may have been open to the north throughout the Pliocene, and was perhaps connected to the North Atlantic via the south during part of the Early and Mid-Pliocene (Funnell 1996; Head 1998). However, low planktonic foraminiferal species diversity in the Coralline Crag Formation suggests a relatively remote connection with the open ocean waters of the North Atlantic (Jenkins *et al.* 1988). Water depths may have reached 50 m or more during deposition of the Ramsholt Member (Hodgson & Funnell 1987; Head 1998; but see Wilkinson 1980).

Palaeoclimatic analyses of fossils from the Coralline Crag Formation provide conflicting results. Some fossil assemblages attest to warm temperate surface waters, often with Mediterranean characteristics (Harmer 1898; Head 1998). Microfaunal assemblages suggest relatively warm temperatures (e.g. Wood *et al.* 1993; see table 1) and reduced seasonality. Jenkins & Houghton (1987) inferred a maximum range of annual temperature of approximately 8°C based on foraminifera (temperature range $10\text{--}18^\circ\text{C}$), whereas bryozoans suggest overall average temperatures varying between 14 and 21°C (Lagaaij 1963; Cheetham 1967). Higher temperatures than at the present day were also suggested by the

smaller zooid sizes found in Coralline Crag populations of several extant bryozoan species compared with living populations (Okamura & Bishop 1988). O'Dea & Okamura (2000) applied MART analysis to 11 bryozoan species, arriving at a mean seasonal temperature variation of 6.6°C, with different species giving values of between 4.6 and 8.9°C (see table 1). By contrast, oxygen isotope values from the mollusc *A. opercularis* yielded sea temperature estimates that are similar to today, ranging from a winter value of *ca* 6.5°C to a summer value of 16.6°C (see Johnson *et al.* 2000; herein tables 1 and 2). This contrasts with the molluscan faunal analysis of Raffi *et al.* (1985), which suggested summer temperatures of '20°C or higher'. However, the Ramsholt Member also yields the bivalve *Arctica islandica*, which in the modern North Sea has a thermal maximum not exceeding 16°C (Witbaard & Bergman 2003). Unpublished $\delta^{18}\text{O}$ data from three well-preserved individuals of *A. islandica* from the Ramsholt Member (E. M. Harper (2008, unpublished data), using an ice volume correction for seawater $\delta^{18}\text{O}$ of -0.35‰) give a temperature range of 3.6–12.8°C, which is consistent with the data from *Aequipecten*.

For estimates of temperature from the shells of Pliocene bivalves in the southern North Sea, there is a potential effect of runoff and intense evaporation (opposite effect) in a restricted marine basin. There was freshwater runoff coming in to the North Sea from the Baltic, Rhine system and English rivers, but the effect would have been to make the O-isotopic composition of the bivalve shells lighter, giving the appearance of higher temperatures (counter to what is recorded from these shells). However, the setting of at least the Ramsholt Member bivalves (offshore in perhaps 50 m of water depth) makes this effect likely to have been small.

In northern Belgium dinoflagellate cyst assemblages from the Kattendijk Formation, which is probably older than the Ramsholt Member of the Coralline Crag Formation (Louwye *et al.* 2004), include several thermophilic taxa that suggest warm conditions in the southern North Sea Basin. By contrast, the overlying Luchtbal Sands and lower part of the Oorderen Sands both yield cool water taxa. The Basal Shelly Unit of the Luchtbal Sands may correlate with a pronounced cold stage at approximately 4 Ma (marine isotope stage Gi16 of Shackleton *et al.* 1995; renamed Gi20 by Liesecki & Raymo 2005, fig. 8). These deposits are correlated stratigraphically, in part, with the Coralline Crag Formation. However, Head (1998), while noting that more than 75 per cent of dinoflagellate taxa from the Coralline Crag Formation are extinct, rendering palaeoenvironmental interpretations based on modern flora uncertain, nonetheless recorded thermophilic taxa. These include persistent *Tectatodinium pellitum*, which has a modern southern temperate to tropical distribution.

7. Marine environmental signals from the Pliocene of eastern North America

The Yorktown Formation of the Carolinas–Virginia comprises sandy clays and shell marls deposited along the Atlantic Coastal Plain. Deposition of the Rushmere/Morgart's Beach Members of this formation (figure 2) represents the most extensive marine transgression in the Pliocene, creating a shallow shelf sea extending from Maryland to Florida (Ward *et al.* 1991). This is consistent with the richest foraminiferan assemblages from the middle part of the formation

(Dowsett & Wiggs 1992). To the south, in subtropical Florida, the Tamiami Formation, at least in part, is the lateral equivalent of the Yorktown Formation (figure 2). Here, the Lower Pinecrest Beds were deposited during the major transgression onto the shelf that produced the Rushmere/Morgart's Beach Members of the Yorktown Formation. There followed a period of marine lowstand, when sea level may have dropped by as much as 50 m (Cronin & Dowsett 1996 and references therein), before the Late Pliocene (Gelasian) successions of the Upper Pinecrest Beds and Chowan River Formation were deposited (figure 2).

(a) *Warm seas north and south of Cape Hatteras*

Ward *et al.* (1991) summarized the Pliocene–Pleistocene molluscan assemblages from Virginia and the Carolinas and interpreted them in terms of warm and cool coastal water masses. As already noted, Cape Hatteras today defines a major faunal boundary in the marine shelf assemblages of the east coast of the USA. Here the southern limit of the modern Virginian cool temperate mollusc faunal province and the northern limit of the Carolinian subtropical molluscan faunal province effectively meet (Ward *et al.* 1991). These provinces are defined by the southwards-flowing cool-water Virginia Current, and the northwards-flowing warm-water Carolina Coastal Current and Florida Current, the latter being deflected towards the ocean at Cape Hatteras as the Gulf Stream. The result of convergence of these warm- and cold-water currents is that the warm temperate regime is eliminated, and the temperate molluscan fauna is greatly reduced (Ward *et al.* 1991).

The faunal provinces of the Pliocene on the east coast were clearly very different for part of this epoch. During the Early Pliocene (Yorktown Formation, Sunken Meadow Member), a cool temperate molluscan fauna in water depths of perhaps 20 m extended from Virginia to the Carolinas (Ward *et al.* 1991, fig. 16-4). The marine transgression that deposited the Rushmere/Morgart's Beach Members of the Yorktown Formation introduced a warm subtropical molluscan fauna to South Carolina, with warm temperate faunas extending from North Carolina to Virginia (Ward *et al.* 1991, fig. 16-4). Much of the Florida Peninsula would have been submerged at this time (equivalent to the time of deposition of Tamiami Formation units 5–10), and Ward *et al.* (1991) speculated that the Gulf Stream was deflected westwards. Finally, the Moore House Member of the Yorktown Formation introduced a warm temperate to subtropical marine molluscan assemblage into Virginia. These patterns of mollusc distribution indicate that for much of the Mid-Pliocene (Rushmere to Moore House Members; see figure 2) warmer waters than at present extended north of Cape Hatteras (see table 1).

The warm water interpretation of the molluscan fauna is supported by evidence from microfauna. Cronin & Dowsett (1990) identified a warm water tropical ostracod fauna in the Duplin Formation of North Carolina, suggesting bottom water temperatures as warm as 18°C for winter and 26°C for summer. Dowsett & Wiggs (1992) used foraminifer assemblages in the Yorktown Formation, especially the common occurrence of *Globigerinoides sacculifer*, in post-Sunken Meadow Member strata, to indicate winter temperatures 3–5°C warmer than but summer temperatures similar to the present day.

Analysis of oxygen isotopes in the bivalves *Carolinapecten* and *Chesapecten* from the Yorktown Formation (Krantz 1990) supports the notion of more equable conditions extending north of Cape Hatteras in the Early and Mid-Pliocene (table 1). These data suggest reduced seasonality, with winter temperatures (*ca* 8.6°C) warmer than those experienced in the coastal waters of modern Virginia (see table 1), but with summer temperatures cooler (*ca* 24°C). Krantz (1990) used ice volume correction factors between -0.3 and -0.6 ppt for seawater $\delta^{18}\text{O}$ to calculate palaeotemperatures (based on polar ice sheets with a reduced volume). We have recalculated palaeotemperatures for this material (table 2) using seawater isotope values generated by GCMs specifically for this region, one for the Early Pliocene ($\delta^{18}\text{O}=0.7\text{‰}$) and another for the Mid-Pliocene ($\delta^{18}\text{O}=1.1\text{‰}$; see figure 4). In both instances our correction factors result in warmer winter temperatures (*ca* 12–14°C, see table 2) and summer temperatures that are similar to present-day summer coastal temperatures in Virginia.

(b) Subtropical Florida

Jones & Allmon (1995, fig. 12) summarized a range of palaeotemperature data for the Pinecrest Beds, comparing these with modern sea temperatures off Florida in water depths from 2 to 35 m. They noted (*op. cit.*, p. 69) that evidence from ostracods (see also below) suggested water temperatures during Pinecrest Beds deposition to be as much as 2.4°C cooler in August and 0.6°C cooler in February. Studies of pollen, foraminifera and ostracods (Willard *et al.* 1993) have supported the interpretation of cooler summer temperatures. To calculate palaeotemperatures from bivalves and gastropods, Jones & Allmon (1995) used a range of different estimates of local seawater $\delta^{18}\text{O}$, including correction factors for the difference between modern and Pliocene ice volume. Values of sea temperature determined from the isotopic composition of the aragonitic bivalve *M. campechiensis* from the middle of the main shell bed in unit 6/7 (Lower Pinecrest Beds), where fully marine conditions pertained, suggest seasonal extremes of temperature of 10.9 and 24.3°C, while values from the gastropod *Turritella* suggest 13–25.7°C. Jones & Allmon (1995, p. 70) favoured palaeotemperatures based on seawater $\delta^{18}\text{O}$ values uncorrected for reduced ice volume, as these provided temperatures (14.2–24.3°C for *Mercenaria* and 16.4–25.7°C for *Turritella*; see table 1) more consistent with interpretations from ostracods and foraminifera (Willard *et al.* 1993). Jones & Allmon (1995, p. 70) noted in general that the isotopic values of molluscs in unit 6/7 were cold-shifted relative to modern temperatures (see also table 1); those from the younger unit 2 were more similar to the present day (non-ice-corrected values for *Turritella* were 16.4–25.7°C). Our recalculations from two of their *Mercenaria* bivalve shells (MC130 and MC121) suggest palaeotemperatures in the range 16–27°C that are very similar to modern values in this region (table 2).

Analysis of ostracod faunas through the interval of the Tamiami Formation to Pleistocene Bermont Formation by Cronin & Dowsett (1996, following on from Cronin & Dowsett 1990) led these authors to infer warmer winters and cooler summers, and a narrower range of seasonal temperature variation compared with today for much of the Pliocene. Although they noted that some of the ostracod faunas had no modern analogues (for example in unit 11), Cronin and Dowsett

were able to suggest cool temperatures for the Early Pliocene (winter temperatures less than 17°C, summer temperatures approx. 22°C). During deposition of the Lower Pinecrest Beds (units 5–10), they interpreted summer temperatures to be typically 21–27°C (total range, but ranges vary from horizon to horizon (Cronin & Dowsett 1996; fig. 4.7, table 4.2)), and winter temperatures that were typically 18–21°C. The dominance of brackish water faunas in the Upper Pinecrest Beds rendered interpretations of water temperature difficult, but Cronin and Dowsett inferred winter and summer temperatures between 17 and 24°C (total range) for the uppermost part of this interval. In general, Pliocene temperatures in Florida appear to have been characterized by slightly cooler summers than at the present day (see tables 1 and 2).

8. Comparison with Pliocene climate models and data from the open oceans

Analysis of sea temperature data gleaned from planktonic foraminifera over longer time intervals for the Pliocene indicates climatic variability, with periodicities associated with secular variations in the Earth's orbit, particularly the 41 kyr obliquity cycle (e.g. Dowsett & Poore 1991). Such detailed interpretation depends on high-resolution data from ocean sites, with sampling of foraminifera at intervals of sediment representing *ca* 10 kyr intervals, and with excellent stratigraphical control (Dowsett & Poore 1991; Dowsett & Robinson 2006). Superimposed on this high-frequency variability are longer-term changes in mean temperature values that delineate distinct intervals when climate was warmer or cooler than today. Thus, Dowsett & Poore (1991, p. 191) identified: (i) an interval in the earlier Pliocene when SSTs were generally cooler than today; (ii) an interval centred around 3.3–3 Ma when temperatures were warmer; and (iii) decreasing SSTs thereafter.

Subsequent analysis of a large palaeontological dataset by the Pliocene Research, Interpretation and Synoptic Mapping (PRISM) Group of the USGS indicated that SSTs at mid and high latitudes were warmer than at the present day, defining the Mid-Pliocene warm period (Dowsett *et al.* 1994, 1999). Within this interval SSTs were under the influence of 'background' high-frequency orbital effects on climate, but were, on the whole, warmer than present. Dowsett *et al.* (1992) noted that faunal data for the North Atlantic indicated SSTs warmer at mid to high latitudes but a little cooler at low latitudes, a signal they interpreted as a response to increased meridional heat transfer from low to high latitude. This pattern of warming at mid and high latitudes with cooling or unchanged SSTs in low latitudes is also manifested in global reconstructions of the Pliocene based on faunal analysis techniques (e.g. Dowsett *et al.* 1999). However, subsequent analysis of palaeoclimatic data from tropical and mid-latitude upwelling regions has suggested warming during the Mid-Pliocene (e.g. Haywood *et al.* 2005; Dekens *et al.* 2007; Dowsett & Robinson 2009). Furthermore, model outputs using coupled ocean–atmosphere models for the Mid-Pliocene (Haywood & Valdes 2004; Haywood *et al.* 2005) indicate a small degree of warming (relative to the pre-industrial era) in general in the tropics, with the largest degree of warming still centred on the high latitudes. Climate model experiments using a coupled OAGCM conducted by Haywood & Valdes

(2004) have shown that high-latitude warming during the Mid-Pliocene may have been strongly influenced by changes in albedo as a result of reduced polar ice sheets, rather than increased meridional heat transfer.

A pattern of slight tropical warming coupled with more dramatic warming at higher latitudes is one that might be anticipated if warming was at least partly a function of increased CO₂ in the atmosphere. The reconciliation of data versus model outputs for the Pliocene tropics must be a major focus for future study, although the difficulties therein are acknowledged with respect to the ability of proxy records to robustly detect SST changes of very small magnitude (i.e. an unfavourable signal-to-uncertainty ratio) and to the fact that in areas such as the western equatorial Pacific suitable calibrations for faunal analysis and alkenone palaeothermometry are not available.

At present, data from fossil organisms occupying the Pliocene shelf seas of the North Atlantic do not resolve the forcing mechanisms of the Mid-Pliocene warm period, and in some instances they provide palaeoclimatic data that are inconsistent with data from oceanic sites. This may be because, in part, they represent time intervals older than the 'warm period' (figure 2). Thus, the faunas of unit 11 in the Tamiami Formation of Florida and its lateral equivalent, the Sunken Meadow Member of the Yorktown Formation, which definitely antedate the Mid-Pliocene warm period (figure 2), preserve a signal of a slightly cooler (though not cold) Pliocene interval (e.g. Krantz 1990; Cronin & Dowsett 1996; see also table 1). Later deposits (Yorktown and Duplin Formations), which incorporate the Mid-Pliocene warm period, provide evidence for a more vigorous transfer of heat from the tropics along the east coast of North America such that warm water penetrated along the coast of Virginia north of Cape Hatteras. This interpretation would support the hypothesis of increased meridional heat transport. This ensured warmer winters throughout much of Yorktown Formation times (see Dowsett & Wiggs 1992, p. 82; herein table 2), and is consistent with climate model reconstructions for the Early and Mid-Pliocene (cf. table 2 data and figure 4).

Cooler summer temperatures off Florida during deposition of the Lower Pinecrest Beds may have been the result of seasonal upwelling of deep water (see Jones & Allmon 1995). This is suggested in the carbon isotope profiles of some shells of the bivalve *Mercenaria* from unit 6/7 of the Lower Pinecrest Beds, which show light carbon values (from deep waters enriched in ¹²C) corresponding to heavy oxygen values (indicating cool water; Jones & Allmon 1995, fig. 9b).

Conditions in the southern North Sea during the Early and Mid-Pliocene are more equivocal. Most of the Coralline Crag Formation seems to have been deposited prior to 3.4 Ma; that is, before peak Mid-Pliocene warming (figure 2). This, in itself, appears to be inconsistent with the model of maximum sea level achieved during the warm period (e.g. Dowsett & Cronin 1990). The explanation may lie in the following: (i) significant local control on relative sea level (see Mathers & Zalasiewicz 1988); (ii) a problem of stratigraphical correlation; (iii) sea-level change associated with a cold glacial stage (e.g. M2, which occurred at approx. 3.4 Ma, around the time that sedimentation of the Coralline Crag may have ceased in the North Sea; see figure 2); or (iv) a combination of these factors.

As noted, signals from different fossil groups in the Coralline Crag Formation provide contrasting records of climate. Wilkinson (1980) summarized fossil evidence from earlier workers, pointing out that the presence of the free-living

bryozoan *Cupuladria*, for example, suggested that winter temperatures did not fall below 14°C (Lagaaij 1963). A warmer North Sea during deposition of the Coralline Crag Formation is also consistent with an enhanced Gulf Stream effect. Indeed, Mid-Pliocene SSTs recorded at NE Atlantic Deep Sea Drilling Project sites 548 and 552 (see figure 1) are significantly warmer than present (Dowsett & Poore 1991, fig. 2; Dowsett *et al.* 1992, fig. 2), by some 5°C in winter months (Dowsett *et al.* 1992, fig. 1). However, there are also indications of Coralline Crag Formation temperatures being similar to or even cooler than the present day (e.g. data from the bivalve *Aequipecten*, see tables 1 and 2; and E. M. Harper 2008, unpublished data). Johnson *et al.* (2000, p. 429) speculated that cool temperature signals from two Coralline Crag Formation valves of *A. opercularis* (see tables 1 and 2) might represent anomalously cold years, or cryptic diagenesis. Their evidence from growth increment analysis of these fossils (with substantially wider increments interpreted as representing summers warmer than present) favoured the latter explanation.

Climate was clearly not static through the period prior to 3 Ma, as evidenced from oxygen isotope records in foraminifera (Dowsett & Poore 1991; Lisiecki & Raymo 2005; Mudelsee & Raymo 2005), and as also displayed in varied palaeoclimate data obtained through detailed sampling of the Pliocene sequence of Florida (e.g. see Cronin & Dowsett 1996, table 4.2). There are a number of possible explanations for the mixed signals in the Coralline Crag Formation. These include: (i) reworking of shells from time intervals when climate was different from (cooler than?) those at the time the sediment was deposited; (ii) the discontinuous nature of the rock record, which may preserve different palaeoclimatic regimes at different places; (iii) sampling at low stratigraphical resolution, with material being imprecisely located in rock successions recording more than one climatic state (as suggested by stratigraphic variation in facies: see Balson *et al.* 1993); and (iv) diagenesis in meteoric waters resetting geochemical signals, as noted by Johnson *et al.* (2000). There is currently no detailed study of diagenetic alteration in bivalve material from the Coralline Crag Formation, although in the context of cement precipitation from meteoric waters (Balson 1983), it is difficult to conceive how shell material could have become ¹⁸O-enriched, thus yielding cool isotopic temperatures.

The Coralline Crag Formation represents sediments deposited above storm wave base in which material was transported and reworked. Wilkinson (1980) estimated depths as little as 20 m for deposition and noted that, for the microfauna, contamination and intermixing of assemblages were major problems for interpretation. The hypothesis of wholesale reworking of larger shells, such as those of terebratulid brachiopods or the bivalve *Arctica*, has not been investigated in detail though Balson *et al.* (1993, p. 69) suggested widespread reworking of shells in the Sudbourne Member (figure 2). However, more recent evaluations of *Arctica* specimens from the Ramsholt Member suggest that in this unit they are well preserved and have not been subject to reworking (E. M. Harper 2008, recent observations). At many localities (e.g. Broom Pit) a particular fossil organism, such as *Arctica*, is seen to be dominant at a particular horizon. The significance of this in terms of environmental change remains to be determined. The complex lithostratigraphy of the Coralline Crag deposits, with intraformational unconformities (Balson *et al.* 1993, p. 63), lends support to the idea that stratigraphically unlocalized material could encompass different

climate regimes, especially if the whole formation represents a time period of greater than 200 000 years (e.g. see stratigraphy of Wood *et al.* 1993, fig. 3), during which high-frequency climatic change may well have occurred (Dowsett *et al.* 2005; Lisiecki & Raymo 2005).

Although data from the Coralline Crag Formation are sometimes inconsistent with the model of warming in the North Atlantic presented by Dowsett *et al.* (1992, 1996, 1999) for the Mid-Pliocene, interpretations of cooler sea temperatures from bivalve data in the Coralline Crag Formation are consistent with climate models for the Early Pliocene that display little or no warming for the North Sea (see figure 4a). They are also consistent with the high variability of NE Atlantic climate identified by Dowsett *et al.* (2005, fig. 6; see also Draut *et al.* 2003) in which SSTs may vary by more than 2°C over geologically short intervals of 5000 years.

9. Conclusions

A review of existing data for Pliocene sequences in Suffolk, eastern England, and along the east coast of North America demonstrates their partial correlation, and in all instances shows that they record time intervals that in part precede peak warmth of the Mid-Pliocene warm period. Analysis of bryozoans, bivalves and microfossils in these deposits shows a northwards shift of subtropical faunas along the coast of the Carolinas–Virginia relative to present day, with reduced seasonality and warm water extending northwards beyond Cape Hatteras: during deposition of the Yorktown Formation winter temperatures were much warmer than at the present day. This observation would support conceptual models of increased meridional heat transport for the Pliocene. Reduced seasonality is also apparent in the southern North Sea, with estimates from ostracods suggesting winter temperatures warmer than 10°C, but estimates from bivalves (*Aequipecten* seasonal range *ca* 6.5–16.6°C) giving values similar to the present day. This mixed signal is a paradox and might be a function of material representative of different (cool and warm) climatic states being mixed.

This review reveals the need for a detailed stratigraphical analysis and sampling of the Coralline Crag Formation, in the manner of that undertaken for the Pinecrest Beds of Florida (e.g. Cronin & Dowsett 1996; Jones & Allmon 1995). In particular, environmental, taphonomic and diagenetic data from bryozoans (MART analysis), ostracods, dinoflagellates, bivalves and brachiopods need to be integrated horizon by horizon. There is also a dearth of oxygen isotope data from bivalves in the Yorktown Formation, and no published detailed data from the Duplin and Raysor Formations of the Carolinas, though both areas bear similar mollusc assemblages (Ward *et al.* 1991). Ongoing work on *Chesapecten* from Florida to Delaware will provide a more complete picture of palaeoclimate along the eastern seaboard of North America during the Mid-Pliocene (Goewert & Surge 2007). These deposits also contain extensive cheilostome bryozoans, and these hold great potential for future MART analysis of Pliocene sequences (Knowles *et al.* 2006).

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